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Basal area growth for 15 tropical tree species in Puerto Rico

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Abstract

The tabonuco forests of Puerto Rico support a diverse population of tree species valued for timber, fuel, food, wildlife food and cover, and erosion control among other uses. Tree basal area growth data spanning 39 years are available on 15 species from eight permanent plots in the Luquillo Experimental Forest. The complexity of the rain forest challenges current forest stand modeling techniques. As a starting point individual tree basal area growth is modeled using the Chapman–Richards function constrained for hypothetical maximum tree size. In addition to initial tree diameter or basal area, significant explanatory variables are crown class, topographic position and degree of ground incline. Plots illustrate the differing growth patterns of the 15 tropical mixed/moist forest species. Two species exhibit exceptional growth. *Buchenavia capitata* (Vahl) Eichl. has basal area growth peaking at 87 cm^2 $year^{-1}$. The *Manilkara bidentata* (A. DC.) A. Chev. data show growth rates in excess of 60 cm^2 $year^{-1}$ and the Chapman–Richards function indicates growth potential to a peak of 122 cm^2 $year^{-1}$.

Keywords: Tabonuco; Chapman–Richards function; Periodic annual increment; Crown class; Topographic position; Degree of ground incline

1. Introduction

Stand dynamics within tropical mixed/moist forests are the most complex in the world. Studies in the tropics of the eastern hemisphere have led to diverse and generally discouraging conclusions concerning growth prediction. Lowe (1966, 1973) concluded that differences in growth rates are only partly due to contemporary influences because trees develop a 'pecking order' while still young. Gerrard (1968) saw little practical potential for the individual tree approach to growth prediction in stands containing a diversity of species and age classes. Mervart (1969, 1972) concluded that the process of growth was sufficiently random to frustrate any attempt to interpret it in deterministic terms, and that the possibility of reducing the error of increment estimates via regression analysis of the girth–increment relationship was quite limited.

In the neo-tropics an early study by Wadsworth (1953), relating tree growth to prior tree size, crown vigor, and surrounding stand density, found only a weak correlation. However, a more recent study by Wadsworth et al. (1989) points to a number of tree increment indicators with potential for accurately predicting individual tree breast height diameter (dbh) or basal area (*ba*) growth. The best indicators were crown diameter (*cd*) and *cd*/dbh ratio in conjunction

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with initial dbh or *ba*. Unfortunately, most tropical tree datasets do not contain crown diameter, but based on the work of Wadsworth et al. this variable should be included in future inventory and measurement work. In the present work crown diameter at the beginning of the growth period was not available. The objective of this study was to investigate other explanatory variables and construct equations for predicting tree basal area growth for 15 of the more commercially and ecologically important species of tabonuco forests in Puerto Rico. These equations should provide a starting point for more detailed investigations of stand and forest growth. It is believed that these 15 species should display similar, though not exact, growth patterns elsewhere in the tropics.

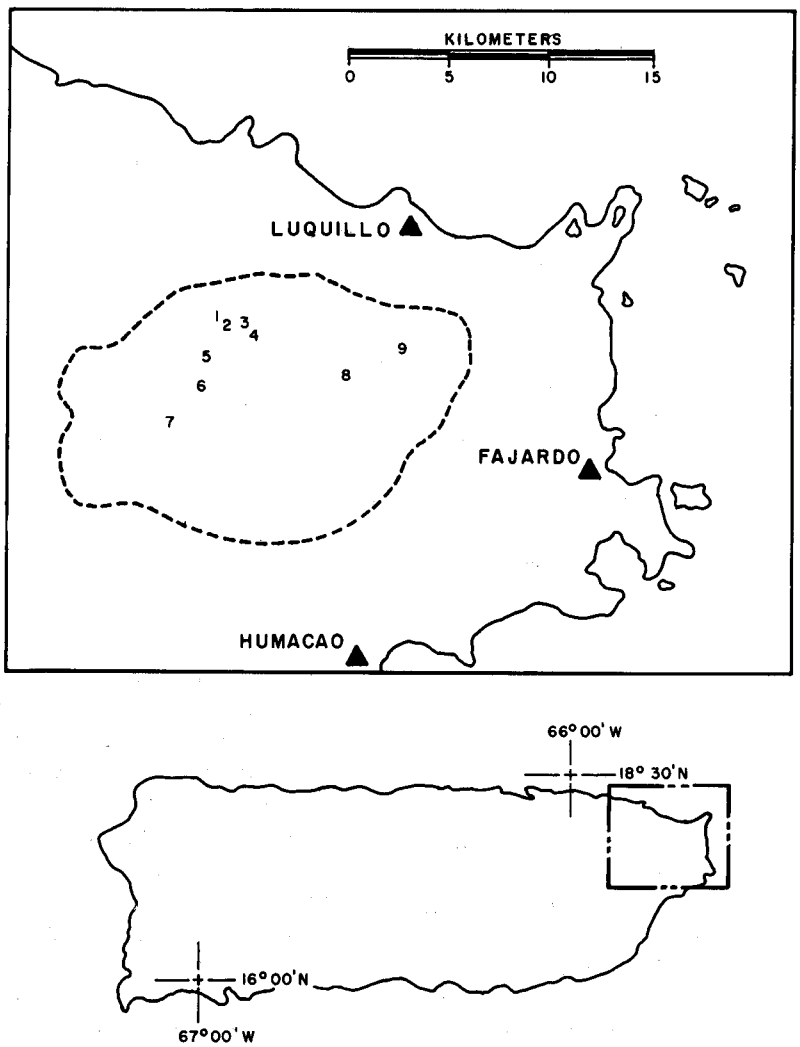

Fig. 1. Location of selected long term growth plots within the Luquillo Experimental Forest in northeastern Puerto Rico. Dashed line in inset represents forest boundary.

Table 1
Descriptive statistics on study sites within the Luquillo Experimental Forest, Puerto Rico

Site[a]	Average elevation (m)	Prevailing aspect	Mean slope (deg.)
1	440	S80E	31
2	500	N75E	37
3	550	N55E	35
5	450	N80E	22
6	640	N70E	16
7	480	N65E	25
8	470	S65E	39
9	200	N60E	33

[a]Site 4 was destroyed during road construction.

2. Study sites

The availability of many hundreds of repeatedly measured trees from eight sites (nine originally established, site 4 destroyed during road construction) within a 20 km^2 area of the Luquillo Experimental Forest in Puerto Rico (Fig. 1) presented an opportunity to model individual tree growth. Sites are briefly described in Table 1. Latitude is 18° N and the elevation of the forests studied range from 200 to 640 m above sea level. The climate, frost-free with rainfall ranging from 250 to 450 cm annually, is classified as subtropical wet and rain forest life zones (sensu Holdridge, 1967). Soils are acid clays and loams, mostly ultisols and inceptisols. The tabonuco forests (so-called because the tabonuco tree (*Dacryodes excelsa* Vahl) is the most prominent species) used are both primary and late secondary, reaching 30 m in height.

3. Data

Permanent remeasurement plots were established in the Luquillo Experimental Forest in 1943. Diameter and crown class (dominant, codominant, intermediate, and suppressed) of all trees were measured (as well as other variables) and for each plot topography (ridge, slope, bottom), aspect (recorded as azimuth), and incline (greatest downward slant, degrees from horizontal) were noted. Trees were remeasured for dbh in 1947, 1952, 1958, 1965, 1976, and 1982, resulting in 39 years of growth measurement. From the pool of data 15 species had sufficient numbers and size range for modeling tree basal area growth. These species were: (1) *Dacryodes excelsa* Vahl; (2) *Tabebuia heterophylla* (DC.) Britton; (3) *Ormosia krugii* Urban; (4) *Buchenavia capitata* (Vahl) Eichl.; (5) *Manilkara bidentata* (A. DC.) A. Chev.; (6) *Matayba domingensis* (DC.) Radlk.; (7) *Didymopanax morototoni* (Aubl.) Decne. & Planch.; (8) *Cecropia peltata* L.; (9) *Inga fastuosa* (L.) Willd.; (10) *Homalium racemosum* Jacq.; (11) *Sloanea berteriana* Choisy; (12) *Linociera domingensis* (Lam.) Knobl.; (13) *Tetragastris balsamifera* (Sw.) Kuntze; (14) *Byrsonima coriacea* (Sw.) DC.; (15) *Guarea guidonia* (L.) Sleumer. The tree data are summarized in Table 2.

4. Methods

If one wishes to obtain an accurate assessment of growth pattern over time, the tree should be measured at short intervals. Therefore I computed periodic annual increments (PAI) for each time interval in the data. That is, I started at interval 1943–1947 and for each tree with a diameter at both time periods I computed a periodic annual basal area increment (*ba* growth divided by number of years). I then computed PAI for the intervals 1947–1952, 1952–1958, 1958–1965, 1965–1976, and 1976–1982. If for a tree a measurement was not made at a measurement period then the PAI was coded as missing for the intervals involved.

Because of its widespread use and familiarity, I settled on the Chapman–Richards growth function to express periodic annual basal area growth. Under this model (Pienaar and Turnbull, 1973) the growth rate of an organism is expressed as the difference between constructive metabolism (anabolic growth) and destructive metabolism (catabolic growth). This function, constrained to equal zero at theoretical maximum tree size

Table 2
Mean sample tree diameters (cm) (±SD) of 15 species in a moist tropical forest in Puerto Rico for seven time periods

Species	1943			1947			1952			1958			1965			1976			1982		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
Dacryodes excelsa Vahl	19.2	12.6	101	27.2	19.3	214	29.4	19.8	212	25.2	13.1	329	33.6	19.4	211	35.1	16.0	138	37.7	17.3	359
Tabebuia heterophylla (DC.) Britton	6.7	1.3	5	11.3	3.3	37	15.0	4.0	35	15.8	4.9	280	17.3	5.0	170	22.1	6.7	231	23.4	7.4	287
Ormosia krugii Urban	11.5	6.7	8	14.9	8.7	37	18.9	9.3	37	20.7	8.5	107	24.2	9.2	61	29.2	9.2	63	31.6	9.7	110
Buchenavia capitata (Vahl) Eichl.	22.2	12.9	6	28.7	15.1	16	35.9	15.3	13	28.5	14.7	45	33.9	15.3	20	41.4	19.9	24	44.1	19.2	50
Manilkara bidentata (A. DC.) A. Chev.	11.5	4.6	47	13.1	5.9	58	15.4	6.3	56	17.9	6.7	115	22.3	8.3	54	30.0	9.6	35	29.1	10.3	119
Matayba domingensis (DC.) Radlk.	–	–	0	12.0	5.7	58	15.1	6.0	57	17.2	5.9	142	20.4	7.3	30	24.2	6.8	63	26.0	7.1	142
Didymopanax morototoni (Aubl.) Decne. & Planch.	18.7	7.9	7	13.0	6.0	30	14.9	6.2	27	17.3	5.7	121	20.3	5.9	75	23.5	6.9	76	25.3	8.3	123
Cecropia peltata L.	17.8	14.5	3	18.2	17.4	11	20.7	16.0	12	20.0	7.4	60	28.9	12.2	22	30.6	10.8	25	32.0	12.5	61
Inga fastuosa (L.) Willd.	17.0	5.3	3	12.8	3.3	8	15.6	4.2	5	17.5	7.1	62	18.3	6.2	39	26.6	9.3	53	28.4	9.9	65
Homalium racemosum Jacq.	6.1	–	1	17.9	12.5	10	19.4	12.3	10	17.6	9.3	38	18.7	6.1	10	26.2	9.4	26	31.8	15.5	42
Sloanea berteriana Choisy	12.6	7.9	14	15.3	9.8	20	18.4	10.1	17	20.0	10.5	40	19.7	7.8	16	24.7	9.6	17	27.6	15.1	44
Linociera domingensis (Lam.) Knobl.	7.3	4.6	4	9.5	2.8	12	11.6	2.9	9	15.2	5.3	41	18.0	–	1	23.2	8.5	19	23.5	7.5	43
Tetragastris balsamifera (Sw.) Kuntze	19.7	12.7	15	21.4	13.1	15	23.7	13.0	15	25.9	13.4	16	27.5	15.0	13	37.8	–	1	33.0	14.7	16
Byrsonima coriacea (Sw.) DC.	5.9	1.0	4	6.9	1.9	4	–	–	0	13.0	3.0	19	16.1	2.9	14	25.0	8.5	15	29.9	10.3	22
Guarea guidonia (L.) Sleumer	–	–	0	–	–	0	12.9	2.3	2	18.1	5.9	10	22.7	6.4	10	32.7	7.9	8	33.2	10.7	10

Table 3
Asymptotic tree basal area, regression coefficients and associated fit statistics from growth models for 15 species in a moist tropical forest in Puerto Rico

Species	A	b_1	b_2	b_3	b_4	b_5	R^2	RMSE
Eq. (1)								
Tabebuia heterophylla	3849	0.31983	0.89421				0.13	8.42
Manilkara bidentata	31416	0.30372	0.93193				0.64	8.53
I. fastuosa	3849	0.64514	0.95038				0.12	13.70
L. domingensis	5027	0.27013	0.89684				0.40	5.74
Eq. (2)								
Dacryodes excelsa	31416	5.94762	0.28608	−0.28976			0.35	12.30
O. krugii	5027	0.45568	0.81041	−0.06587			0.34	10.27
Matayba domingensis	2828	1.78329	0.57596	−0.20575			0.36	7.31
Tetragastris balsamifera	7854	4.51702	0.43270	−0.45533			0.69	8.17
Eq. (3)								
Buchenavia capitata	17672	1.29601	0.72459	−3.01103	0.54071	0.50262	0.51	22.18
Didymopanax morototoni	2828	0.53916	0.67774	0.23697	−0.76755	−0.99593	0.13	8.92
C. peltata	5027	3.78875	0.28512	1.98154	−2.45468	0.46728	0.30	17.91
H. racemosum	7854	0.37467	0.72026	−1.31511	2.22638	2.93882	0.50	10.20
S. berteriana	11310	0.13564	0.77037	2.32871	−0.60188	0.46750	0.31	10.46
Byrsonima coriacea	2828	0.70093	0.56782	0.90109	0.60853	0.0[a]	0.44	5.25
G. guidonia	13274	0.69385	0.65432	−0.24530	0.30781	1.14116	0.32	19.84

Note: A is asymptote value (cm^2); b_i's are regression coefficients; R^2 is the variation explained in the dependent variable, calculated as $1-\Sigma(y_i-\hat{y})/\Sigma(y_i-\bar{y})$; and RMSE is root mean square error (cm^2).
[a]There were no trees occurring in a bottom type topography for this species.

(Shifley and Brand, 1984), is

$$\Delta X/\Delta t = b_1(X^{b_2} - X/A^{(1-b_2)}) \quad (1)$$

where $\Delta X/\Delta t$ is PAI, X is tree basal area (cm^2), t is time (for this study Δt is always 1 year), A is asymptotic tree basal area—the point where basal area growth equals zero, and b_1 and b_2 are equation coefficients. This function is usually presented as a differential equation; however, the discrete nature of the data makes a difference equation more appropriate.

Additional variables available for modeling were crown class (CC) (Smith, 1962), degree of incline (INCL), topography (TOPO), and aspect. I ran a series of multiple nonlinear regressions using initial basal area and various combinations of the above variables to predict PAI. I found that CC (coded as: 1, dominant; 2, codominant; 3, intermediate; 4, suppressed) and the interaction of INCL with the class variable TOPO improved the prediction for some species. Therefore, two additional models were formulated

$$\Delta X/\Delta t = b_1(X^{b_2} - X/A^{(1-b_2)})\exp(b_3 CC) \quad (2)$$

$$\Delta X/\Delta t = b_1(X^{b_2} - X/A^{(1-b_2)})\exp[(b_3 + b_4 I_1 + b_5 I_2)\mathrm{INCL}/100] \quad (3)$$

where INCL is degrees from the horizontal (i.e. in the range 0–90) and $I_1=1$ if TOPO is classified as slope else $I_1=0$ and $I_2=1$ if TOPO is classified as bottom else $I_2=0$. If both I_1 and I_2 equal zero then we are left with b_3 which is the effect of ridge topography. The coefficient b_4 measures the differential effect between ridge and slope topography and b_5 measures the differential effect between ridge and bottom topography. If incline is measured in percent, then values can be converted to degrees for use in Eq. (3) with the formula: degrees = cotan(percent/100).

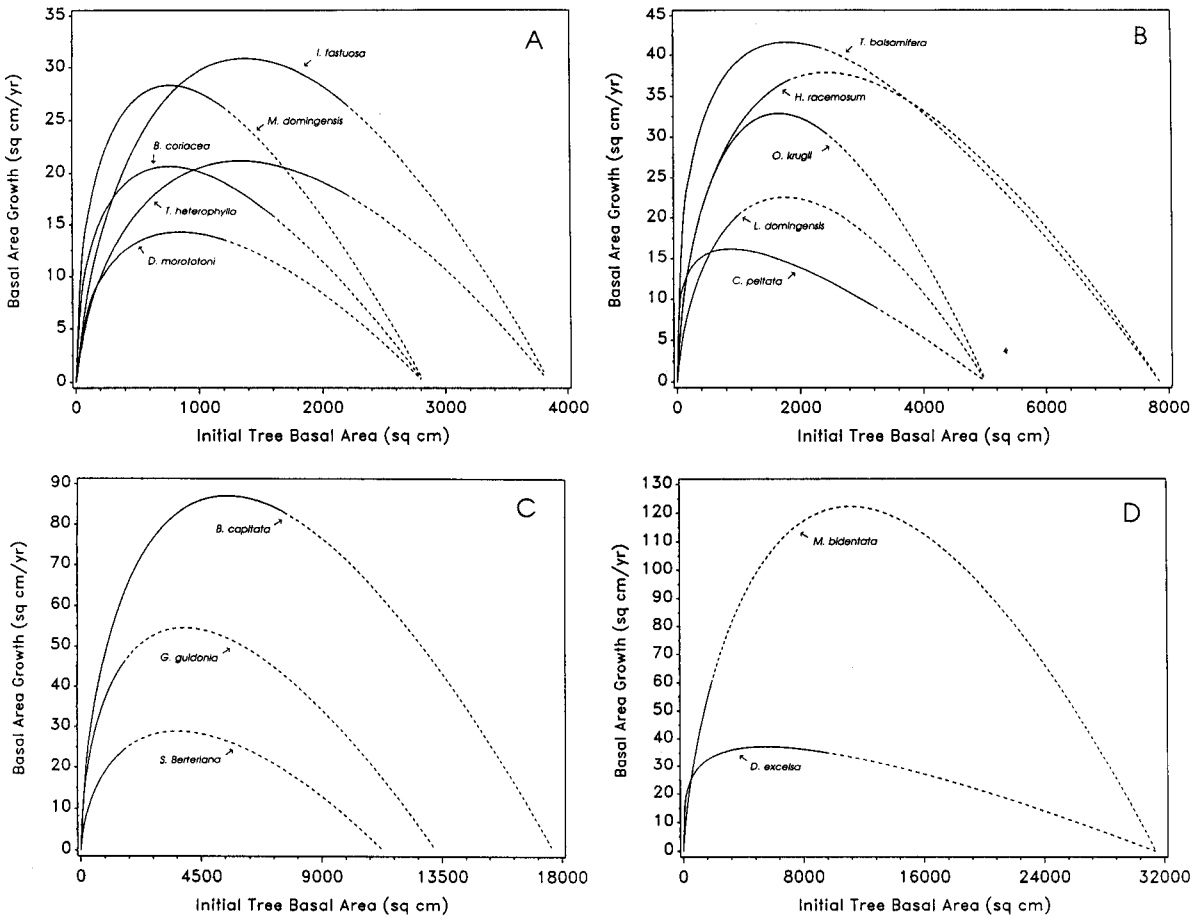

Fig. 2. Comparative growth rate curves of 15 species in a mixed/moist tropical forest in Puerto Rico. Species were grouped into (A) small, (B) medium, (C) large, and (D) very large tree sizes. Solid lines show extent of actual data, dashed lines are extrapolations.

5. Results and discussion

The data from each species were fitted to the three equations via nonlinear least squares and residuals were examined for departures from regression assumptions. The most appropriate equation for a given species was determined from the residual analyses as well as the variation explained in the dependent variable (R^2). The equation giving the highest R^2 was not necessarily judged as best though in most cases (13 of 15) this held true. Table 3 lists asymptote values (F.H. Wadsworth, International Institute of Tropical Forestry, USDA Forest Service, Rio Piedras, Puerto Rico, personal communication, 1994), equation coefficients, and fit statistics. Four species (*I. fastuosa*, *L. domingensis*, *Manilkara bidentata*, and *Tabebuia heterophylla*) did best under Eq. (1), the standard Chapman–Richards function. Additional variables did not improve predictions. For four species (*Dacryodes excelsa*, *M. domingensis*, *O. krugii*, *Tetragastris balsamifera*), the addition of *CC* provided sufficient improvement to warrant inclusion. Finally, for the remaining seven species, the TOPO by INCL interaction contributed

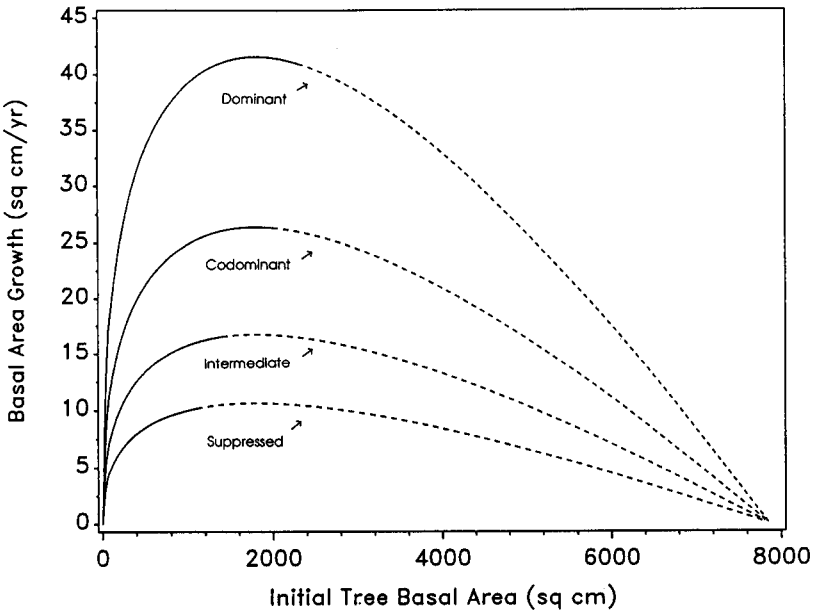

Fig. 3. Illustration of growth rate response across crown class. Species is *Tetragastris balsamifera* in a moist tropical forest in Puerto Rico. Solid lines show extent of actual data, dashed lines are extrapolations.

enough explanatory power to justify its use.

Plots illustrating comparative growth rates of these species are given in Fig. 2. Species were grouped by their asymptote values as (A) small, (B) medium, (C) large, and (D) very large. For species under Eq. (2) the dominant crown class was used. This shows the best response for those species. For the eight sites the overall average degree of incline was close to 30 so this value was used for INCL in Eq. (3) coupled with slope topography ($I_1=1$, $I_2=0$). Keep in mind that for the seven species under Eq. (3) plotted in Fig. 2, the curves shown are one of many possible responses. The growth rate of each species is shown by a solid line followed by a dashed line which shows the extent of the actual data and extrapolation to the asymptote, respectively. One general trend that is immediately obvious is that the maximum growth rate range from group A to group D steadily increases. For group A maximum rates range from 14 to 31 $cm^2\ year^{-1}$, for group B from 16 to 42 $cm^2\ year^{-1}$, for group C from 29 to 87 $cm^2\ year^{-1}$, and for group D from 37 to 122 $cm^2\ year^{-1}$. All species exhibit unique growth rate patterns, none of the 15 species overlap (except for *O. krugii* and *H. racemosum* for tree basal area size less than 800 cm^2). For five of the species, namely *H. racemosum*, *L. domingensis*, *G. guidonia*, *S. berteriana*, and *Manilkara bidentata*, the growth rates from the available data had not peaked. The dashed line portions of the growth rate curves of these five species in Fig. 2 are an extensive extrapolation beyond the range of the data and represent the least squares best 'guess' of the growth rate trend to the asymptote. The fitted equations for these five species should be used with caution.

The species *Buchenavia capitata* had the best growth from actual data, peaking at 87 $cm^2\ year^{-1}$. *Buchenavia capitata* is a large, spreading timber tree that occurs throughout the Caribbean islands, Panama and South America from Venezuela to French Guiana, Brazil, and Bolivia. The wood is reported to be of good quality, moderately heavy (specific gravity 0.61), and strong (Little and Wadsworth, 1964). The tree is also used for shade. Based on this growth analysis and its ecological and commercial impor-

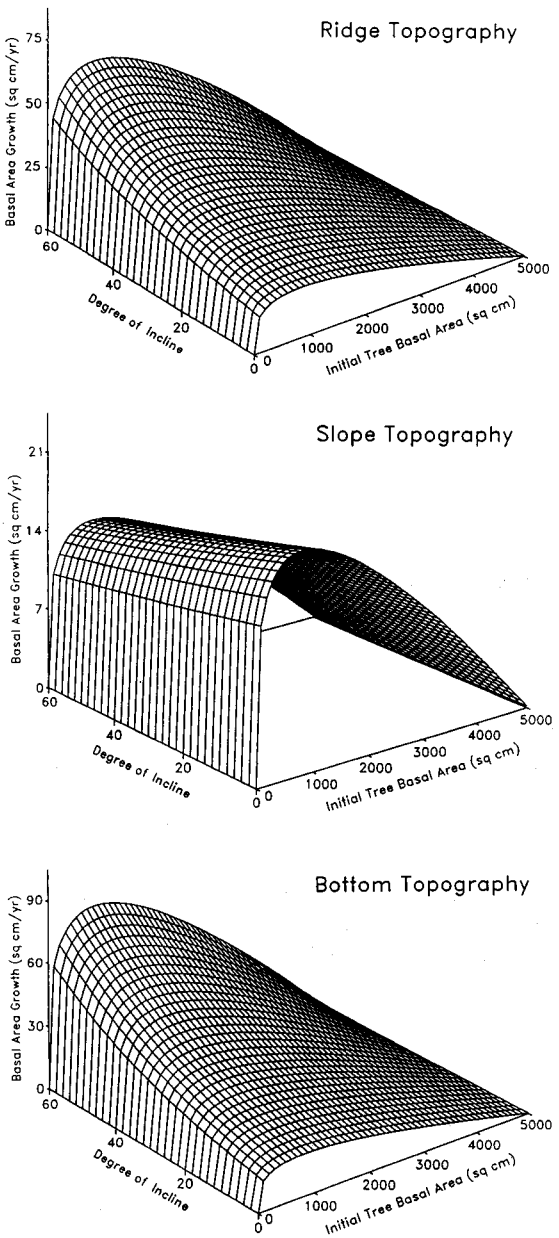

Fig. 4. Illustration of growth rate response surfaces by topographic position. Species is *Cecropia peltata* in a moist tropical forest in Puerto Rico. Maximum observed *ba* values were 1700 cm^2, 3200 cm^2, and 2800 cm^2 for ridge, slope, and bottom topography, respectively. Observed ground incline ranged from 12 to 42°, 16–64°, and 25–51° for ridge, slope, and bottom topography, respectively.

tance, this species has much to recommend it.

The species *Manilkara bidentata* shows the highest growth potential. Actual data exhibit growth rates in excess of 60 cm^2 $year^{-1}$ and the fitted function extrapolates growth to a peak of 122 cm^2 $year^{-1}$. Additional research is needed, with data from older and larger trees, to see if this growth rate can actually be obtained. However, these initial results are very encouraging. Little and Wadsworth (1964) report this species as slow growing, which seems contrary to the results of this study. *Manilkara bidentata* occurs throughout the Caribbean, Panama, and northern South America from the Guianas and Venezuela to Peru and Northern Brazil. The wood is very hard, heavy (specific gravity 0.82), and extremely strong. The milky sap of this species is the source of balata gum, and the species is also used for shade.

As mentioned, four species showed significant trends with crown class. *Tetragastris balsamifera* is plotted in Fig. 3 to demonstrate the response curve by crown class. The family of curves show the substantial effect on growth going from one canopy position to another. The response surfaces of *C. peltata* are shown in Fig. 4 to depict the wide range of responses possible for those species sensitive to topographic position and the amount of ground incline. In ridge and bottom topography increasing ground incline greatly improves PAI. However, other species have different response surface shapes molded by the occurrence of positive and negative b_3 through b_5 coefficients. For example, *H. racemosum* has a negative b_3 coefficient so increasing degree of ground incline in ridge topography would result in decreasing PAI. Each of the seven species under Eq. (3) has a unique set of response surfaces.

6. Conclusions

From this study of the growth rate trends of 15 tropical species within a mixed/moist forest, one can see the effects on growth from the complex mix of physiography and stand dynamics. I will leave it to tropical ecologists and foresters to investigate why some species are sensitive to

ground inclination and topography and others more to canopy position. Ultimately crown diameter may be the best indicator of growth, according to Wadsworth et al. (1989), and this should be investigated more fully. The Chapman–Richards model provides a flexible framework for investigating species growth, capable of incorporating many independent variables.

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